Genetic Guidelines for Fisheries Management

Abridged Version

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Fish are the product of their genes, the environment and of the interaction between the two. The genetics of fish, in connection with the environment, determine the quality and persistence of the fishery resource. Often, managers have concentrated on manipulating non-genetic, environmental aspects of fisheries (e.g., stocking, harvest control, and habitat management) without regard to the genetic makeup of fish stocks. This is particularly unfortunate because relatively minor changes in management practices might sustain the genetic integrity of a stock.

Maintaining genetic variation is important to fish stocks. Genetic variation gives populations the ability to adapt to changing environments. The genetic diversity in a population is a finite resource that can be used up. For example, humans can "spend" the genetic diversity in populations by widespread stocking of a genetically similar (homogeneous) hatchery population. The long-term impact of such "spending" on the perpetuation of the population is uncertain at best and detrimental at worst. It is important to rationally integrate the conservation of genetic variation and the stewardship of fisheries resources.

The material covered in both the abridged and unabridged versions of ***Genetic Guidelines for Fisheries Management*** lays the foundation for this process. Part 1 of this synopsis identifies various management activities and explains how they might affect the genetics of fish stocks. Genetic terms and principles are further defined in Part II. Part III describes the tools used to gather genetic data and their applications to fisheries management and research.

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Hatchery Management Influences the Genetics and Fitness of Hatchery Stocks

Wise hatchery managers maintain **genetic variation** in breeding populations while producing fish that are suitable for their intended use. Poor hatchery practices can reduce **genetic diversity** through random **genetic drift** and alter **selection** pressures on broodstocks. Mating techniques, **inbreeding**, and other selection pressures associated with domestication affect the genetics and fitness (reproductive success and survival) of hatchery stocks.

Populations lose genetic diversity and become increasingly inbred at a rate inversely proportional to their **effective population size (N_e)**, therefore, smaller populations tend to lose genetic diversity more rapidly. Uneven sex ratios and large differences in the numbers of offspring produced by each parent also reduce N_e. Hatchery managers can increase N_e, and thus reduce inbreeding and losses of genetic diversity by starting with and maintaining large broodstocks, mating with equal sex ratios, and equalizing or minimizing differences in family size.

Hatchery environments will inevitably be different from natural environments and consequently put different selection pressures on fish. These domestication pressures can be caused by intentional cultivation of certain traits (e.g., faster growth), inadvertent selection for traits due to non-random broodstock collection or unnatural rearing conditions, or by relaxing natural selection pressures because fish are no longer subject to a wild environment. Many of these selective changes are unavoidable but could be reduced by randomly collecting large numbers of broodstock and mimicking more natural rearing conditions in the hatchery.

The Case of the Reduced Spawning Efficiency

How could the effective population size of a lake trout broodstock (N_e) be less than the number spawning (N)? Researchers found the spawning efficiency (N_e/N) of some broodstocks fell as low as 0.10 (only one out of ten potential breeders actually contributed to the next generation). Theoretically, these broodstocks with such inefficient spawning lose variation at rates up to 10 times faster than broodstocks where all potential breeders equally spawn.

The researchers attributed the less-than-ideal spawning efficiencies to unequal sex ratios at spawning (often males outnumbered females by two times) and the practice of pooling eggs and sperm from multiple parents. When sperm are pooled, those of one male often fertilize the majority of eggs, thus reducing or eliminating genetic contributions by other males.

Page, K.S. 2001. Genetic Diversity and Interrelationships of Wild and Hatchery Lake Trout in the Upper Great Lakes: Inferences for Broodstock Management and Development of Restoration Strategies. Master's Thesis. Michigan State University, East Lansing, MI.

Stocked and Transplanted Fish Influence the Genetics of Wild Stocks

It is possible that stocked fish will be less fit (able to contribute to next generation) than wild fish at a particular location. This is especially true for stock transfers but may also be true for hatchery-reared fish derived from the local population. Stocked fish could affect the fitness and long-term adaptability of wild populations. Stocked fish could hybridize with native fish, resulting in the loss of genetic diversity between populations and **outbreeding depression**. Stocked fish also influence indirect genetic pressures. Stocking encourages increased fishing activity, which in turn increases the harvest of wild fish mingling with the stocked fish. Also, stocked fish could introduce new diseases to wild stock or displace native fish, thereby reducing the range of natural populations.

Ways to reduce the genetic risks imposed by stocked fish and to help insure that stocked fish have high fitness include:

1) Select source fish on the basis of three similarity criteria: *similarity in genetic lineage, similarity in life history patterns, and similarity in ecology of the originating environment.*
2) Obtain broodstock by sampling randomly from spawners in a wild population to avoid inadvertent selection for body size, spawning time, etc.
3) Aim at maximizing effective population size through mating schemes and hatchery management.
4) Minimize the hatchery-rearing period for broodstock and production stock. The consequences of hatchery culture (i.e., domestication, inadvertent selection and inbreeding) accumulate with time.
5) Simulating natural conditions (e.g., substrate, cover, underwater feeding) in the hatchery may increase the fitness of stocked fish upon release.
6) Stock fish at a size, time, and place so that they are similar to wild fish and integrate with wild fish rather than displace them.

The Case of the Missing Fish

Why did only one hatchery steelhead survive for every five surviving naturalized steelhead? We studied genetic interactions between naturalized (self-sustaining in the wild) and hatchery steelhead on Minnesota's North Shore of Lake Superior. In our experiments, we compared the relative survival of offspring from crosses of naturalized and hatchery adults, and hybrids between the strains. Not only did we find that naturalized steelhead survive about five times more than their hatchery kin, but we also found that the survival of hybrid offspring was about half that of naturalized offspring. We concluded that intermating with this strain of hatchery fish may reduce the fitness of naturalized steelhead populations in Lake Superior.

Miller, L.M. and A.R. Kapuscinski. Local adaptation and outbreeding depression in naturalized rainbow trout populations stocked with hatchery fish. Manuscript in preparation.

Harvest Management Influences the Genetics of Wild Stocks

Harvest pressures and alteration of spawning habitats may directly reduce population size and the effective population size, thus theoretically increasing the rate of loss of genetic variation. Harvest and habitat alteration may also alter demographic factors (skewed sex ratio and increased variance in family size) that reduce the effective population size. For example, because growth rates can differ between the sexes, size regulations or angler selection might preferentially target one sex and skew the sex ratio. Disturbances on spawning grounds might destroy the offspring of entire families and increase the variance in reproductive success among adults.

Many fisheries amount to artificial selection programs that act on fitness-related traits or traits genetically correlated with fitness. Harvested fish are seldom a random sample from the population because fishing techniques and gear select individuals with certain characteristics. Consequently, fish that avoid the dinner table will be different than the average fish in the population before human exploitation. If the differences are **heritable**, then the next generation will be genetically and phenotypically different from the previous generation. This process can occur in every generation until substantial changes have occurred in the population. It is possible that inadvertent artificial selection will produce a stock of fish with inferior commercial value or reduced fitness.

The Case of the Fourth Generation

Why were the sizes of Atlantic silversides different after four generations? Researchers from the State University of New York-Stony Brook simulated the genetic effects of fishing on laboratory populations of Atlantic silversides. They "harvested" by removing either the largest or smallest fish in the populations, mimicking the effect of size-selective fishing gear or size regulations. In only four generations, the selected populations had substantially decreased or increased in size due to genetic selection. Furthermore, for populations in which large fish were removed (typical of many fisheries) yields were significantly reduced after only a few generations.

Conover, D.O. and S.B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science, July 5, 297:94-96.

Habitat Alteration Influences the Genetics of Wild Stocks

A consequence of environmental changes that reduce habitat (e.g., spawning stream obstruction), kill fish (e.g., pollution) or limit reproductive success (e.g., acid rain) is a decrease in the effective population size. In addition, habitat alterations can fragment populations into isolated smaller populations subjected to higher losses of genetic diversity.

Natural selection helps fish populations adapt to altered environments but related consequences should be kept in mind. Fish adapted to the new environment (e.g., tolerant of polluted water) may not be desirable for human consumption. Productivity of the population may remain low even after the population adapts to new conditions. Many generations might elapse before the population adapts to the new environment because the response to natural selective pressures may be slow. The population may never adapt if the environment changes more rapidly than its ability to evolve.

The Case of the Impassible Dam

Would it be prudent to help bull trout over an impassible dam? Researchers from University of Montana thought it would be. They studied the effects of a dam on migratory bull trout populations in the Clark Fork River knowing that the bull trout population above the dam was declining. With genetic techniques they showed that fish gathering below the dam were probably hatched in streams above the dam then washed down river. Because of this genetic similarity to fish above the dam, they suggested that the risk of outbreeding depression associated with passing adults over dams in the Clark Fork system would be minimal compared to the potential genetic and demographic benefits to populations above the dams.

Neraas, L.P. and P. Spruell. 2001. Fragmentation of riverine systems: the genetic effects of dams on bull trout (Salvelinus confluentus) *in the Clark Fork River system. Molecular Ecology 10:1153-64.*

Genetic Engineering and Ecological Risk

Genetically modified organisms (GMOs) may impose ecological risks if they are introduced or escape into the natural environment. Although most GMO fish have been developed for aquaculture purposes, many culture systems are extremely vulnerable to accidental releases into the natural environment (e.g., damage to ocean net pens, flooding of outdoor ponds). Each line of GMO fish should be evaluated for potential ecological risks imposed by escapees. These risks include increased invasiveness of an alien (exotic) species or gene flow from GMOs to wild relatives. Gene flow may homogenize population genetic differences or in extreme cases, as simulations have shown, cause populations to go extinct. It is essential to understand how the novel traits cultivated in GMO fish could alter the probability or severity of consequences they might impose on natural populations should they escape and hybridize. To determine this, risk analysis of GMOs requires evaluation of the net fitness of potential escapees.

Measures to reduce the ecological risks imposed by GMO fish can focus on preventing escapes or reducing impacts if escapes occur. Physical barriers (e.g., lethal water temperatures or pH) or mechanical barriers (e.g., screens) can be used to prevent escapes. Biological barriers, such as induced triploidy, which makes adults of some fish species functionally sterile, can be used to reduce gene flow and invasive species risks. But sterilization does not necessarily neutralize environmental risks. Escaped, sterile fish might still compete with wild fish for limited resources or engage in courtship and spawning behavior, disrupting breeding in wild populations.

The Case of the Trojan Gene

What could happen if GMO fish escaped and hybridized with wild fish? To explore this question researchers at Purdue University developed a model known as the "Trojan gene effect." If a transgenic fish line exhibits a large mating advantage that overwhelms a moderate survival disadvantage compared to wild relatives, their model predicts a dramatic outcome. The mating advantage drives the transgenes into the wild population, spreading them rapidly throughout the population, but the lower survival of each consecutive generation carrying the transgenes erodes the population size. Unless the decline is stemmed by human intervention or by sufficiently strong, counteracting natural selection, the population will go extinct.

Muir, W.M. and R.D. Howard. 1999. Possible ecological risks of transgenic organism release when transgenes affect mating success: sexual selection and the Trojan gene hypothesis. Proceedings of the National Academy of Sciences USA 96: 13853-13856.

Part II. Genetics Terms* and Principles

Allele—one of the alternative forms of the same gene; alleles for the same gene occur at the same locus.

Gene—a segment of DNA that occupies a specific position (**locus**) on a chromosome, is heritable and has one or more specific effects upon the phenotype of an organism.

Genetic diversity—may be used synonymously or considered just the genetic variation within a species, including within and between population components.

Genetic variation—all the variation due to differences in alleles and genes in an individual, population, or species.

Genotype—the set of alleles at one or more loci in an organism; the entire set of genes carried by an individual.

Phenotype—the visible or measurable traits or characteristics of an organism.

Measures of genetic diversity

Within populations

Allelic diversity—the number of different alleles in a population.

Heritability—the fraction of the total phenotypic variance (variation in a trait, e.g., growth rate, run timing) in a population that is due to the additive effects of genes; used to predict the response to selection. Ranges from 0 to 1, where 1 implies total genetic determination of variation in the trait and 0 implies no heritable genetic determination (e.g., all differences due to environment or genetic effects not predictably inherited through generations).

Heterozygosity—the proportion of individuals in a population that are **heterozygous** (i.e., have two different alleles) at a particular locus, loci, or the entire genome; perhaps the most common measure of genetic variation.

Between populations

Fixation index (F_{ST})—the proportion of the variation at a locus attributable to divergence among populations. Used to determine the amount of **genetic structure** among populations.

Genetic distance—a statistical measure of the genetic similarity between two populations; often used to perform **cluster analyses** that group together samples that are similar and separate those that are dissimilar. Results are typically displayed as branching **tree diagrams (dendrograms)** or other plots that visually group like populations.

Genetic structure—the arrangement of the gene pool of a species into groups of subpopulations that mate randomly within themselves with little or no gene flow between each other.

*Definitions from *Kapuscinski, A.R. and L.M. Miller. 2003. Genetic Guidelines for Fisheries Management. University of Minnesota Sea Grant Program, and Hallerman, E.M. 2003. Population Genetics: Principles and Applications for Fisheries Scientists, American Fisheries Society.*

Forces that change genetic diversity in populations

Effective population size (N_e)—the size of an ideal population that would experience **genetic drift** and **inbreeding** at the same rate (mathematically, 1/2 N_e) as the real population under consideration; reduced by population bottlenecks, uneven sex ratios, and large differences in family size. Because N_e is typically less than the actual population size, real populations tend to lose genetic variation through drift and become increasingly inbred at a faster rate than the actual population size would suggest.

Gene flow—the exchange of genes among populations.

Genetic drift—random changes in allelic frequencies due to natural sampling errors (i.e., a finite number of offspring) that occur in each generation; causes an inevitable reduction in genetic variation as alleles are lost (i.e., no offspring are produced or survive to pass on an allele). The rate of genetic drift increases as **effective population size** decreases.

Migration—the movement of individuals or gametes between populations, followed by successful reproduction and **gene flow** between populations; can increase genetic variation within local populations but may homogenize population differences.

Mutation—a change in the DNA or chromosomes of a cell or organism; the ultimate source of all genetic diversity.

Selection—the natural or artificial process by which breeders are chosen from a population on the basis of fitness or phenotypic value; will often reduce genetic variation when one allele confers the highest fitness but may maintain variation when selection favors different alleles in different or changing environments.

Concerns about genetic diversity

Evolutionary potential—the long-term ability of a population to evolve and thereby persist in the face of environmental change; maintenance of evolutionary potential requires existence of genetic variation in the population. Genetic variation among populations may allow the species to adapt to environmental change. Some local populations may go extinct but the area may be recolonized from populations better suited for the changed conditions. Specific concerns that derive from genetic mechanisms include **inbreeding** and **outbreeding depression**.

Within populations

Inbreeding—the mating of related individuals; in an immediate generation it can result from close kin mating preferentially; over generations it can result from small population size leading to closer relationships among individuals over time, therefore the rate of inbreeding increases as **effective population size** decreases.

Inbreeding depression—a reduction in fitness or vigor due to **inbreeding**, resulting from decreased heterozygosity or expression of deleterious recessive alleles.

Between populations

Outbreeding depression—the phenomenon of reduction in fitness following intraspecific hybridization (matings between individuals from different populations of the same species), either in the immediate hybrids or delayed until later generations; can be attributed to loss of local adaptation or breakdown of co-adapted gene complexes (sets of genes that work efficiently together).

Part III. Genetic Tools for Fisheries Applications

Laboratory Techniques

Genetic markers—characteristics that can be used to infer the genotype of an organism; may be phenotypic characters (e.g., pigmentation), allozymes, chromosome bands, or molecule based. **Molecular genetic markers** directly reveal variation at the DNA sequence level. Genetic markers can be used to determine genotypes and allele frequencies for various genetic analyses or they may be used as tags (i.e., alternative to physical or chemical tags) to track individuals or their offspring.

Allozymes—variant alleles at a protein (enzyme) locus; the first, and still common, laboratory-analyzed genetic marker.

mtDNA—small circular loop of DNA found in the mitochondria of cells; inherited from the mother only so useful for describing female-based genetic processes. Typically analyzed by **restriction digestion** (restriction fragment length polymorphisms, RFLP) or **sequencing**.

Nuclear DNA—chromosomal DNA found in the cell nucleus. Many types of markers based on repetitive DNA sequences (microsatellites, minisatellites), single nucleotide polymorphisms (SNPs), randomly amplified polymorphic DNA (RAPDs), digestion and random amplification (AFLP) and other amplification or restriction digestion procedures.

Polymerase chain reaction (PCR)—a molecular genetic technique used to greatly amplify the number of copies of a targeted DNA sequence so that further analyses are possible; has the potential to amplify DNA from very small and degraded tissues (e.g., dried fish scales, minute fin clips, a single fish fry), simplifying sample collection and allowing for analysis of archived tissue collections.

Restriction enzymes—cleave DNA at specific sequences called recognition sites. Genetic variation (sequence differences) at recognition sites will determine whether or not the enzyme can cut. Different patterns of cutting as revealed by **gel electrophoresis** reveal underlying genetic variation.

Gel electrophoresis—a laboratory procedure for the separation and observation of proteins (allozymes) or DNA; separates allelic forms so that genotypes can be inferred.

Applications of Genetic Tools

Hybridization—species-specific genetic markers can be used to identify species and hybrids between species. Markers have been used to identify populations free from detrimental interbreeding with alien species.

Stock identification—allele frequency differences can distinguish reproductively isolated populations (stocks). Managers should avoid or carefully control mixed-stock fisheries to avoid overexploiting weaker stocks. On a broader geographic scale, markers can identify genetic population structure, or genetic relationships among populations. Managers might use this information to avoid transplanting stocks that show large genetic differences.

Parentage—genetic markers provide heritable tags that can be used to assign offspring back to their parents. Used to track stocked fish when physical tagging is unfeasible and to compare individual reproductive success in the natural environment.

Forensics—markers, especially those based on PCR, can be used to identify the species of fish parts and products. They may also identify the lake or region from which a fish was taken.

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